

Apatosaurus

Apatosaurus (/əˌpætəˈsɔːrəs/^[3]^[4] meaning "deceptive lizard") is a genus of herbivorous sauropod dinosaur that lived in North America during the Late Jurassic period. Othniel Charles Marsh described and named the first-known species, *A. **ajax***, in 1877, and a second species, *A. **louisae***, was discovered and named by William H. Holland in 1916. *Apatosaurus* lived about 152 to 151 million years ago (mya), during the late Kimmeridgian to early Tithonian age, and are now known from fossils in the Morrison Formation of modern-day Colorado, Oklahoma, New Mexico, Wyoming, and Utah in the United States. *Apatosaurus* had an average length of 21–22.8 m (69–75 ft), and an average mass of 16.4–22.4 t (16.1–22.0 long tons; 18.1–24.7 short tons). A few specimens indicate a maximum length of 11–30% greater than average and a mass of 32.7–72.6 t (32.2–71.5 long tons; 36.0–80.0 short tons).

The cervical vertebrae of *Apatosaurus* are less elongated and more heavily constructed than those of *Diplodocus*, a diplodocid like *Apatosaurus*, and the bones of the leg are much stockier despite being longer, implying that *Apatosaurus* was a more robust animal. The tail was held above the ground during normal locomotion. *Apatosaurus* had a single *claw* on each forelimb and three on each hindlimb. The *Apatosaurus* skull, long thought to be similar to *Camarasaurus*, is much more similar to that of *Diplodocus*. *Apatosaurus* was a generalized browser that likely held its head elevated. To lighten its vertebrae, *Apatosaurus* had *air sacs* that made the bones internally full of holes. Like that of other diplodocids, its tail may have been used as a whip to create loud noises.

The skull of *Apatosaurus* was confused with that of *Camarasaurus* and *Brachiosaurus* until 1909, when the holotype of *A. louisae* was found, and a complete skull just a few meters away from the front of the neck. Henry Fairfield Osborn disagreed with this association, and went on to mount a skeleton of *Apatosaurus* with a *Camarasaurus* skull cast. *Apatosaurus* skeletons were mounted with speculative skull casts until 1970, when McIntosh showed that more robust skulls assigned to *Diplodocus* were more likely from *Apatosaurus*.

Apatosaurus is a genus in the family Diplodocidae. It is one of the more basal genera, with only *Amphicoelias* and possibly a new, unnamed genus more primitive. While the subfamily Apatosaurinae was named in 1929, the group was not used *validly* until an extensive 2015 study. Only *Brontosaurus* is also in the subfamily, with the other genera being considered synonyms or reclassified as diplodocines. *Brontosaurus* has long been considered a junior synonym of *Apatosaurus*; its type species was reclassified as *A. excelsus* in 1903. A 2015 study concluded that *Brontosaurus* is a valid genus of sauropod distinct from *Apatosaurus*, but not all paleontologists agree with this division. As it existed in North America during the late Jurassic, *Apatosaurus* would have lived alongside dinosaurs such as *Allosaurus*, *Camarasaurus*, *Diplodocus*, and *Stegosaurus*.



 Apatosaurus Temporal range: Late Jurassic, 152–151 Ma
 PreЄ Є O S

D

C

P

T

J

K

PgN

Contents

Description

Discovery and species

Valid species

Reassigned species

Classification

Palaeobiology

Neck posture

Physiology

Growth

Juveniles

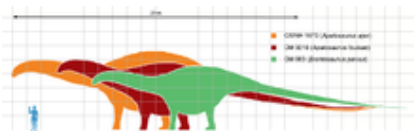
Tail

Paleoecology

References

External links

Description



Comparison of *A. ajax* (orange) and *A. louisae* (red) with a human (blue) and *Brontosaurus parvus* (green)

Apatosaurus was a large, long-necked, quadrupedal animal with a long, whip-like tail. Its forelimbs were slightly shorter than its hindlimbs. Most size estimates are based on specimen CM 3018, the type specimen of *A. louisae*. In 1936 this was measured to be 21.8 m (72 ft), by measuring the vertebral column.^[5] Current estimates are similar, finding that the individual was 21–22.8 m (69–75 ft) long and had a mass of 16.4–22.4 t (16.1–22.0 long tons; 18.1–24.7 short tons).^{[6][7][8]} A 2015 study that estimated the mass of volumetric models of *Dreadnoughtus*, *Apatosaurus*, and *Giraffatitan* estimates CM 3018 at 21.8–38.2 t (21.5–37.6 long tons; 24.0–42.1 short

tons), similar in mass to *Dreadnoughtus*.^[9] Past estimates have put the creature's mass as high as 35.0 t (34.4 long tons; 38.6 short tons).^[6] Some specimens of *A. ajax* (such as OMNH 1670) represent individuals 11–30% longer, suggesting masses twice that of CM 3018 or 32.7–72.6 t (32.2–71.5 long tons; 36.0–80.0 short tons), potentially rivalling the largest titanosaurs.^[10]

The skull is small in relation to the size of the animal. The jaws are lined with spatulate (chisel-like) teeth suited to an herbivorous diet.^[11] The snout of *Apatosaurus* and similar diplodocoids is squared, with only *Nigersaurus* having a squarer skull.^[12] The braincase of *Apatosaurus* is well preserved in specimen BYU 17096, which also preserved much of the skeleton. A phylogenetic analysis found that the braincase had a morphology similar to those of other diplodocoids.^[13] Some skulls of *Apatosaurus* have been found still in articulation with their teeth. Those teeth that have the enamel surface exposed do not show any scratches on the surface; instead, they display a sugary texture and little wear.^[12]



A. ajax skull, specimen CMC VP 7180

Like those of other sauropods, the neck vertebrae are deeply bifurcated; they carried neural spines with a large trough in the middle, resulting in a wide, deep neck.^[11] The vertebral formula for the holotype of *A. louisae* is 15 cervicals, 10 dorsals, 5 sacrats, and 82 caudals. The caudal vertebra number may vary, even within species.^[5] The cervical vertebrae of *Apatosaurus* and *Brontosaurus* are stouter and more robust than those of other diplodocids and were found to be most similar to *Camarasaurus* by Charles Whitney Gilmore.^{[5][14]} In addition, they support cervical ribs that extend farther towards



Cervical vertebra of *A. ajax*
(holotype, YPM 1860) in side and
anterior view

the ground than in diplodocines, and have vertebrae and ribs that are narrower towards the top of the neck, making the neck nearly triangular in cross-section.^[14] In *Apatosaurus louisae*, the atlas-axis complex of the first cervicals is nearly fused. The dorsal ribs are not fused or tightly attached to their vertebrae and are instead loosely articulated.^[5] *Apatosaurus* has ten dorsal ribs on either side of the body.^[15] The large neck was filled with an extensive system of weight-saving air sacs. *Apatosaurus*, like its close relative *Supersaurus*, has tall neural spines, which make up more than half the height of the individual bones of its vertebrae. The shape of the tail is unusual for a diplodocid; it is comparatively slender because of the rapidly decreasing height of the vertebral spines with increasing distance from the

hips. *Apatosaurus* also had very long ribs compared to most other diplodocids, giving it an unusually deep chest.^[16] As in other diplodocids, the tail transformed into a whip-like structure towards the end.^[5]

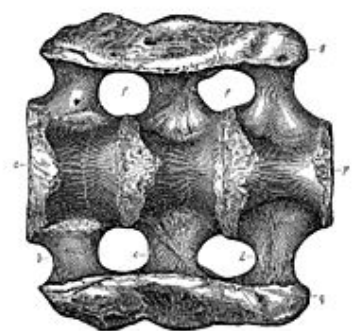
The limb bones are also very robust.^[16] Within *Apatosaurinae*, the scapula of *Apatosaurus louisae* is intermediate in morphology between those of *A. ajax* and *Brontosaurus excelsus*. The arm bones are stout, so the humerus of *Apatosaurus* resembles that of *Camarasaurus*, as well as *Brontosaurus*. However, the humeri of *Brontosaurus* and *A. ajax* are more similar to each other than they are to *A. louisae*. In 1936 Charles Gilmore noted that previous reconstructions of *Apatosaurus* forelimbs erroneously proposed that the radius and ulna could cross; in life they would have remained parallel.^[5] *Apatosaurus* had a single large claw on each forelimb, a feature shared by all sauropods more derived than *Shunosaurus*.^{[5][17]} The first three toes had claws on each hindlimb. The phalangeal formula is 2-1-1-1-1, meaning the innermost finger (phalanx) on the forelimb has two bones and the next has one.^[18] The single manual claw bone (ungual) is slightly curved and squarely truncated on the anterior end. The pelvic girdle includes the robust ilia, and the fused (co-ossified) pubes and ischia. The femora of *Apatosaurus* are very stout and represent some of the most robust femora of any member of Sauropoda. The tibia and fibula bones are different from the slender bones of *Diplodocus* but are nearly indistinguishable from those of *Camarasaurus*. The fibula is longer and slenderer than the tibia. The foot of *Apatosaurus* has three claws on the innermost digits; the digit formula is 3-4-5-3-2. The first metatarsal is the stoutest, a feature shared among diplodocids.^{[5][19]}



Artistic interpretation of *A. louisae*

Discovery and species

The first *Apatosaurus* bones were discovered by Edward Drinker Cope and the name *Apatosaurus ajax* was coined in 1877 by Cope's rival Othniel Charles Marsh, Professor of Paleontology at Yale University, based on a nearly complete skeleton (holotype, YPM 1860) discovered in the eastern foothills of the Rocky Mountains in Gunnison County, Colorado.^{[15][20][21]} The composite term *Apatosaurus* comes from the Greek words *apatē* (ἀπάτη)/*apatēlos* (ἀπατηλός) meaning "deception"/"deceptive", and *sauros* (σαῦρος) meaning "lizard";^[22] thus, "deceptive lizard". Marsh gave it this name based on the chevron bones, which are dissimilar to those of other dinosaurs; instead, the chevron bones of *Apatosaurus* showed similarities with those of mosasaurs.^{[20][23]} During excavation and transportation, the bones of the holotype skeleton were mixed with those of another *Apatosaurus* individual originally described as *Atlantosaurus immanis*; as a consequence, some elements cannot be ascribed to either specimen with confidence.^[21] Marsh distinguished the new genus *Apatosaurus* from *Atlantosaurus* on the basis of the number of sacral vertebrae, with *Apatosaurus* possessing three and *Atlantosaurus* four. Two years later, Marsh announced the discovery of a larger and more complete specimen at Como Bluff, Wyoming. He gave this specimen a new name based on the conventions of his age and the relatively sparse fossil record available at that time. It was later recognised that the features he had used to distinguish



A. ajax sacrum, illustrated in 1879

genera and species were in fact more widespread among sauropods.^{[15][21]} He named the new species *Brontosaurus excelsus*.^[24] All specimens currently considered *Apatosaurus* were from the Morrison Formation, the location of the excavations of Marsh and Cope.^[25]



Obsolete mount of an apatosaurine (possibly *Apatosaurus*) specimen AMNH 460 with sculpted skull, American Museum of Natural History

Another specimen, in the American Museum of Natural History under specimen number 460, which is occasionally assigned to *Apatosaurus*, is considered nearly complete; only the head, feet, and sections of the tail are missing, and it was the first sauropod skeleton mounted.^[26] The specimen was found north of Medicine Bow, Wyoming, in 1898 by Walter Granger, and took the entire summer to extract.^[27] To complete the mount, sauropod feet that were discovered at the same quarry and a tail fashioned to appear as Marsh believed it should – but which had too few vertebrae – were added. In addition, a sculpted model of what the museum thought the skull of this massive creature might look like was made. This was not a delicate skull like that of *Diplodocus* – which was later found to be more accurate – but was based on "the biggest, thickest, strongest skull bones, lower jaws and tooth crowns from three different quarries".^{[5][15][26][28]} These skulls were likely those of *Camarasaurus*, the only other sauropod for which good skull

material was known at the time. The mount construction was overseen by Adam Hermann, who failed to find *Apatosaurus* skulls. Hermann was forced to sculpt a stand-in skull by hand. Osborn said in a publication that the skull was "largely conjectural and based on that of *Morosaurus*" (now *Camarasaurus*).^[29]

In 1903 Elmer Riggs published a study that described a well-preserved skeleton of a diplodocid from the Grand River Valley near Fruita, Colorado, Field Museum of Natural History specimen P25112. Riggs thought that the deposits were similar in age to those of the Como Bluff in Wyoming from which Marsh had described *Brontosaurus*. Most of the skeleton was found, and after comparison with both *Brontosaurus* and *Apatosaurus ajax*, Riggs realized that the holotype of *A. ajax* was immature, and thus the features distinguishing the genera were not valid. Since *Apatosaurus* was the earlier name, *Brontosaurus* should be considered a junior synonym of *Apatosaurus*. Because of this, Riggs recombined *Brontosaurus excelsus* as *Apatosaurus excelsus*. Based on comparisons with other species proposed to belong to *Apatosaurus*, Riggs also determined that the Field Columbian Museum specimen was likely most similar to *A. excelsus*.^[15]



Apatosaurine mount (FMNH P25112) in the Field Museum of Natural History in the 1950s, with its original, inaccurately reconstructed skull

Despite Riggs' publication, Henry Fairfield Osborn, who was a strong opponent of Marsh and his taxa, labeled the *Apatosaurus* mount of the American Museum of Natural History *Brontosaurus*.^{[29][30]} Because of this decision the name *Brontosaurus* was commonly used outside of scientific literature for what Riggs considered *Apatosaurus*, and the museum's popularity meant that *Brontosaurus* became one of the best known dinosaurs, even though it was invalid throughout nearly all of the 20th and early 21st centuries.^[31]



Side view of *A. louisae* CM 3018 mounted with a cast of skull CM 11162

It was not until 1909 that an *Apatosaurus* skull was found during the first expedition, led by Earl Douglass, to what would become known as the Carnegie Quarry at Dinosaur National Monument. The skull was found a short distance from a skeleton (specimen CM 3018) identified as the new species *Apatosaurus louisae*, named after Louise Carnegie, wife of Andrew Carnegie, who funded field research to find complete dinosaur skeletons in the American West. The skull was designated CM 11162; it was very similar to the skull of *Diplodocus*.^[30] Another smaller skeleton of *A. louisae* was found nearby CM 11162 and CM 3018.^[32] The skull was accepted as belonging to the *Apatosaurus* specimen by Douglass and Carnegie Museum

director William H. Holland, although other scientists – most notably Osborn – rejected this identification. Holland defended his view in 1914 in an address to the Paleontological Society of America, yet he left the Carnegie Museum

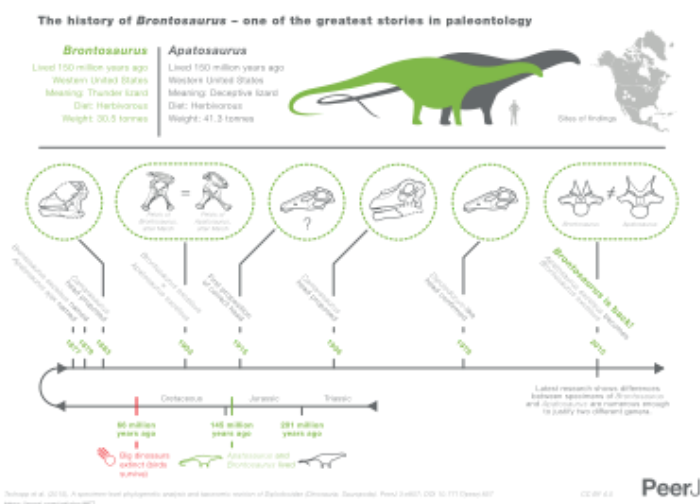
mount headless. While some thought Holland was attempting to avoid conflict with Osborn, others suspected Holland was waiting until an articulated skull and neck were found to confirm the association of the skull and skeleton.^[29] After Holland's death in 1934, museum staff placed a cast of a *Camarasaurus* skull on the mount.^[30]

While most other museums were using cast or sculpted *Camarasaurus* skulls on *Apatosaurus* mounts, the Yale Peabody Museum decided to sculpt a skull based on the lower jaw of a *Camarasaurus*, with the cranium based on Marsh's 1891 illustration of the skull. The skull also included forward-pointing nasals – something unusual for any dinosaur – and fenestrae differing from both the drawing and other skulls.^[29]

No *Apatosaurus* skull was mentioned in literature until the 1970s when John Stanton McIntosh and David Berman redescribed the skulls of *Diplodocus* and *Apatosaurus*. They found that though he never published his opinion, Holland was almost certainly correct, that *Apatosaurus* had a *Diplodocus*-like skull. According to them, many skulls long thought to pertain to *Diplodocus* might instead be those of *Apatosaurus*. They reassigned multiple skulls to *Apatosaurus* based on associated and closely associated vertebrae. Even though they supported Holland, it was noted that *Apatosaurus* might have possessed a *Camarasaurus*-like skull, based on a disarticulated *Camarasaurus*-like tooth found at the precise site where an *Apatosaurus* specimen was found years before.^[28] On October 20, 1979, after the publications by McIntosh and Berman, the first true skull of *Apatosaurus* was mounted on a skeleton in a museum, that of the Carnegie.^[30] In 1998 it was suggested that the Felch Quarry skull that Marsh had included in his 1896 skeletal restoration instead belonged to *Brachiosaurus*.^[33] In 2011 the first specimen of *Apatosaurus* where a skull was found articulated with its cervical vertebrae was described. This specimen, CMC VP 7180, was found to differ in both skull and neck features from *A. louisae*, but shared many features of the cervical vertebrae with *A. ajax*.^[34] Another well-preserved skull is Brigham Young University specimen 17096, a well-preserved skull and skeleton, with a preserved braincase. The specimen was found in Cactus Park Quarry in western Colorado.^[13]



Skull of BYU 17096 ("Einstein") in front view



Infographic explaining the history of *Brontosaurus* and *Apatosaurus* according to Tschopp et al. 2015

Almost all modern paleontologists agreed with Riggs that the two dinosaurs should be classified together in a single genus. According to the rules of the ICZN (which governs the scientific names of animals), the name *Apatosaurus*, having been published first, has priority as the official name; *Brontosaurus* was considered a junior synonym and was therefore long discarded from formal use.^{[35][36][37][38]} Despite this, at least one paleontologist – Robert T. Bakker – argued in the 1990s that *A. ajax* and *A. excelsus* were in fact sufficiently distinct for the latter to merit a separate genus.^[39]

In 2015 Emanuel Tschopp, Octávio Mateus, and Roger Benson released a paper on diplodocoid systematics, and proposed that genera could be diagnosed by thirteen differing characters, and species separated based on six. The minimum number for generic separation

was chosen based on the fact that *A. ajax* and *A. louisae* differ in twelve characters, and *Diplodocus carnegiei* and *D. hallorum* differ in eleven characters. Thus, thirteen characters were chosen to validate the separation of genera. The six differing features for specific separation were chosen by counting the number of differing features in separate specimens generally agreed to represent one species, with only one differing character in *D. carnegiei* and *A. louisae*, but five differing features in *B. excelsus*. Therefore, Tschopp et al. argued that *Apatosaurus excelsus*, originally classified as *Brontosaurus excelsus*, had enough morphological differences from other species of *Apatosaurus* that it warranted being reclassified as a separate genus again. The conclusion was based on a comparison of 477

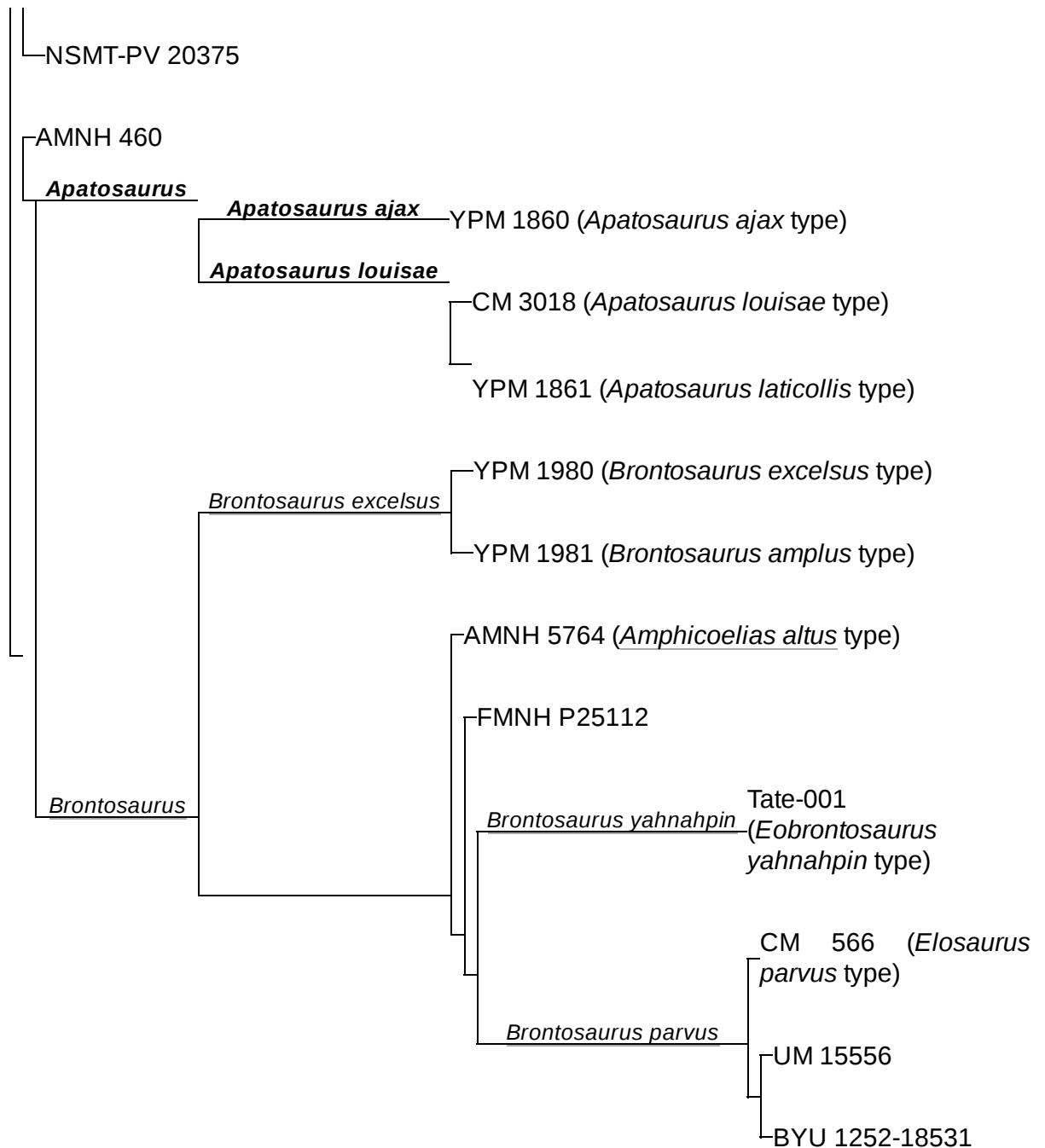
Valid species

A large, complete skeleton of a Tyrannosaurus Rex is the central focus, standing on a raised platform. The skeleton is dark in color, possibly due to staining or the material of the bones. The museum hall is dimly lit, with spotlights illuminating the dinosaur. In the background, other exhibits and museum displays are visible, though less distinct.

Specimen NSMT-PV 20375,
National Museum of Nature
and Science, which may be
A. ajax or a new species

Apatosaurinae

YPM 1840 ("*Atlantosaurus*" *immanis* type)



Reassigned species

- *Apatosaurus grandis* was named in 1877 by Marsh in the article that described *A. ajax*. It was briefly described, figured, and diagnosed.^[5] Marsh later mentioned it was only provisionally assigned to *Apatosaurus* when he reassigned it to his new genus *Morosaurus* in 1878.^[44] Since *Morosaurus* has been considered a synonym of *Camarasaurus*, *C. grandis* is the oldest-named species of the latter genus.^[45]
- *Apatosaurus excelsus* was the original type species of *Brontosaurus*, first named by Marsh in 1879. Elmer Riggs reclassified *Brontosaurus* as a synonym of *Apatosaurus* in 1903, transferring the species *B. excelsus* to *A. excelsus*. In 2015 Tschopp, Mateus, and Benson argued that the species was distinct enough to be placed in its own genus, so they reclassified it back into *Brontosaurus*.^[21]



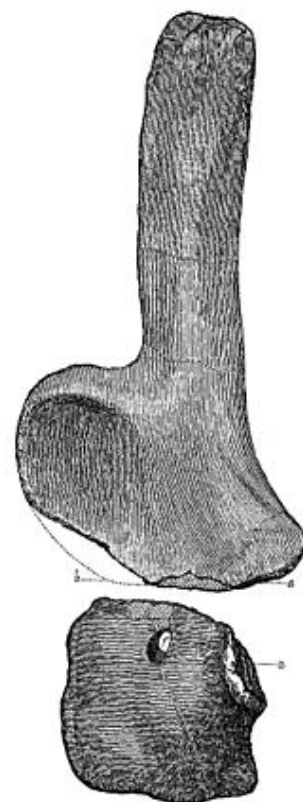
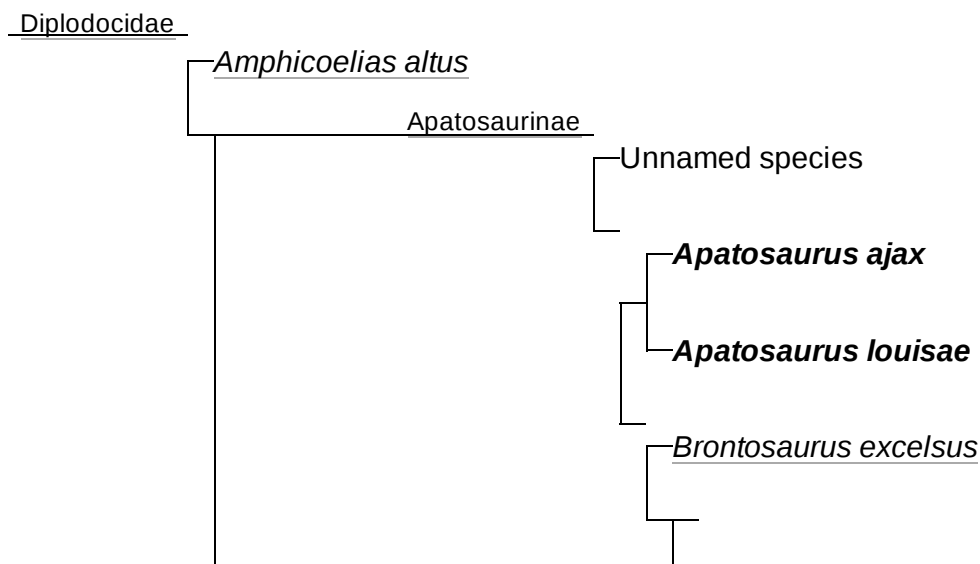
The most complete specimen known to date, *A. sp.* BYU 17096 nicknamed "Einstein"

- *Apatosaurus parvus*, first described from a juvenile specimen as *Elosaurus* in 1902 by Peterson and Gilmore, was reassigned to *Apatosaurus* in 1994, and then to *Brontosaurus* in 2015. Many other, more mature specimens were assigned to it following the 2015 study.^[21]
- *Apatosaurus minimus* was originally described as a specimen of *Brontosaurus* sp. in 1904 by Osborn. In 1917 Henry Mook named it as its own species, *A. minimus*, for a pair of ilia and their sacrum.^{[5][46][47]} In 2012 Mike P. Taylor and Matt J. Wedel published a short abstract describing the material of *A. minimus*, finding it hard to place among either Diplodocoidea or Macronaria. While it was placed with *Saltasaurus* in a phylogenetic analysis, it was thought to represent instead some form with convergent features from many groups.^[47] The study of Tschopp et al. did find that a camarasaurid position for the taxon was supported, but noted that the position of the taxon was found to be highly variable and there was no clearly more likely position.^[21]
- *Apatosaurus alenquerensis* was named in 1957 by Albert-Félix de Lapparent and Georges Zbyweski. It was based on post cranial material from Portugal. In 1990 this material was reassigned to *Camarasaurus*, but in 1998 it was given its own genus, *Lourinhasaurus*.^[19] This was further supported by the findings of Tschopp et al. in 2015, where *Lourinhasaurus* was found to be sister to *Camarasaurus* and other camarasaurids.^[21]
- *Apatosaurus yahnahpin* was named by James Filla and Patrick Redman in 1994. Bakker made *A. yahnahpin* the type species of a new genus, *Eobrontosaurus* in 1998,^[39] and Tschopp reclassified it as *Brontosaurus yahnahpin* in 2015.^[21]

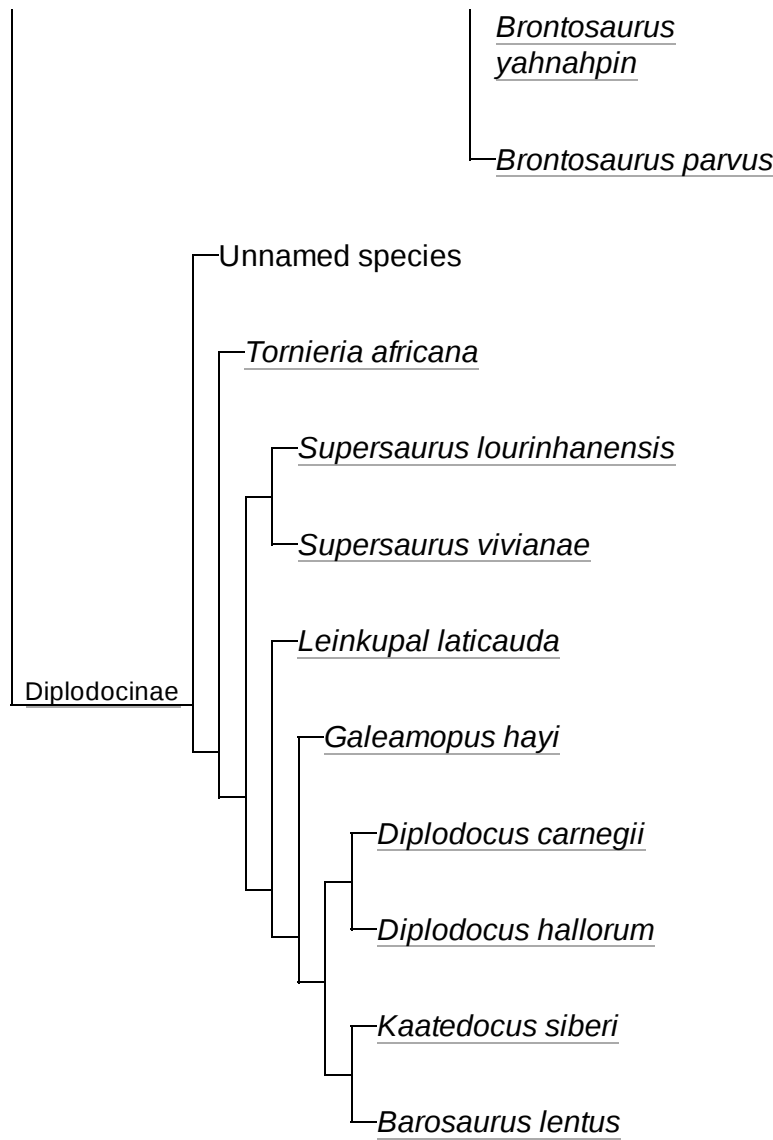
Classification

Apatosaurus is a member of the family Diplodocidae, a clade of gigantic sauropod dinosaurs. The family includes some of the longest creatures ever to walk the earth, including *Diplodocus*, *Supersaurus*, and *Barosaurus*. *Apatosaurus* is sometimes classified in the subfamily Apatosaurinae, which may also include *Suuwassea*, *Supersaurus*, and *Brontosaurus*.^{[16][48][49]} Othniel Charles Marsh described *Apatosaurus* as allied to *Atlantosaurus* within the now-defunct group Atlantosauridae.^{[15][20]} In 1878 Marsh raised his family to the rank of suborder, including *Apatosaurus*, *Atlantosaurus*, *Morosaurus* (= *Camarasaurus*) and *Diplodocus*. He classified this group within Sauropoda, a group he erected in the same study. In 1903 Elmer S. Riggs said the name Sauropoda would be a junior synonym of earlier names; he grouped *Apatosaurus* within Opisthocoelia.^[15] Sauropoda is still used as the group name.^[19] In 2011, John Whitlock published a study that placed *Apatosaurus* a more basal diplodocid, sometimes less basal than *Supersaurus*.^{[50][51]}

Cladogram of the Diplodocidae after Tschopp, Mateus, and Benson (2015).^[21]



Shoulder blade and coracoid of *A. ajax*



Palaeobiology

It was believed throughout the 19th and early 20th centuries that sauropods like *Apatosaurus* were too massive to support their own weight on dry land. It was theorized that they lived partly submerged in water, perhaps in swamps. More recent findings do not support this; sauropods are now thought to have been fully terrestrial animals.^[52] A study of diplodocid snouts showed that the square snout, large proportion of pits, and fine, subparallel scratches of the teeth of *Apatosaurus* suggests it was a ground-height, nonselective browser.^[12] It may have eaten ferns, cycadeoids, seed ferns, horsetails, and algae.^[53] Stevens and Parish (2005) speculate that these sauropods fed from riverbanks on submerged water plants.^[54]



Tracks of a juvenile

A 2015 study of the necks of *Apatosaurus* and *Brontosaurus* found many differences between them and other diplodocids, and that these variations may have shown that the necks of *Apatosaurus* and *Brontosaurus* were used for intraspecific combat.^[14] Various uses for the single claw on the forelimb of sauropods have been proposed. One suggestion is that they were used for defense, but their shape and size make this unlikely. It was also possible they were for feeding, but the most probable use for the claw was grasping objects such as tree trunks when rearing.^[17]

Trackways of sauropods like *Apatosaurus* show that they may have had a range of around 25–40 km (16–25 mi) per day, and that they could potentially have reached a top speed of 20–30 km (12–19 mi) per hour.^[11] The slow locomotion of sauropods may be due to their minimal muscling, or to recoil after strides.^[55] A trackway of a juvenile has led some to believe that they were capable of bipedalism, though this is disputed.^{[56][57]}

Neck posture

Diplodocids like *Apatosaurus* are often portrayed with their necks held high up in the air, allowing them to browse on tall trees. Some studies state diplodocid necks were less flexible than previously believed, because the structure of the neck vertebrae would not have allowed the neck to bend far upwards, and that sauropods like *Apatosaurus* were adapted to low browsing or ground feeding.^{[53][54][58]}

Other studies by Taylor find that all tetrapods appear to hold their necks at the maximum possible vertical extension when in a normal, alert posture; they argue the same would hold true for sauropods barring any unknown, unique characteristics that set the soft tissue anatomy of their necks apart from that of other animals. *Apatosaurus*, like *Diplodocus*, would have held its neck angled upwards with the head pointing downwards in a resting posture.^{[59][60]} Kent Stevens and Michael Parrish (1999 and 2005) state *Apatosaurus* had a great feeding range; its neck could bend into a U-shape laterally.^[53] The neck's range of movement would have also allowed the head to feed at the level of the feet.^[54]



Artistic interpretation of an individual of *A. louisae* arching its neck down to drink

Matthew Copley et al. (2013) dispute this, finding that large muscles and cartilage would have limited movement of the neck. They state the feeding ranges for sauropods like *Diplodocus* were smaller than previously believed, and the animals may have had to move their whole bodies around to better access areas where they could browse vegetation. As such, they might have spent more time foraging to meet their minimum energy needs.^{[61][62]} The conclusions of Copley et al. are disputed by Taylor, who analyzed the amount and positioning of intervertebral cartilage to determine the flexibility of the neck of *Apatosaurus* and *Diplodocus*. He found that the neck of *Apatosaurus* was very flexible.^[59]

Physiology

Given the large body mass and long neck of sauropods like *Apatosaurus*, physiologists have encountered problems determining how these animals breathed. Beginning with the assumption that, like crocodilians, *Apatosaurus* did not have a diaphragm, the dead-space volume (the amount of unused air remaining in the mouth, trachea, and air tubes after each breath) has been estimated at about 0.184 m³ (184 l) for a 30 t (30 long tons; 33 short tons) specimen. Paladino calculates its tidal volume (the amount of air moved in or out during a single breath) at 0.904 m³ (904 l) with an avian respiratory system, 0.225 m³ (225 l) if mammalian, and 0.019 m³ (19 l) if reptilian.^[63]

On this basis, its respiratory system would likely have been parabronchi, with multiple pulmonary air sacs as in avian lungs, and a flow-through lung. An avian respiratory system would need a lung volume of about 0.60 m³ (600 l) compared with a mammalian requirement of 2.95 m³ (2,950 l), which would exceed the space available. The overall thoracic volume of *Apatosaurus* has been estimated at 1.7 m³ (1,700 l), allowing for a 0.50 m³ (500 l), four-chambered heart and a 0.90 m³ (900 l) lung capacity. That would allow about 0.30 m³ (300 l) for the necessary tissue.^[63] Evidence for the avian system in *Apatosaurus* and other sauropods is also present in the pneumaticity of the vertebrae. Though this plays a role in reducing the weight of the animal, Wedel (2003) states they are also likely connected to air sacs, as in birds.^[64]



Tail vertebrae of specimen FMNH P25112, showing pneumatic fossae (holes)

James Spotila et al. (1991) concludes that the large body size of sauropods would have made them unable to maintain high metabolic rates because they would not have been able to release enough heat.^[65] They assumed sauropods had a reptilian respiratory system. Wedel says that an avian system would have allowed it to dump more heat.^[64] Some scientists state that the heart would have had trouble sustaining sufficient blood pressure to oxygenate the brain.^[52] Others suggest that the near-horizontal posture of the head and neck would have eliminated the problem of supplying blood to the brain because it would not have been elevated.^[53]

James Farlow (1987) calculates that an *Apatosaurus*-sized dinosaur about 35 t (34 long tons; 39 short tons) would have possessed 5.7 t (5.6 long tons; 6.3 short tons) of fermentation contents.^[66] Assuming *Apatosaurus* had an avian respiratory system and a reptilian resting-metabolism, Frank Paladino et al. (1997) estimate the animal would have needed to consume only about 262 liters (58 imp gal; 69 U.S. gal) of water per day.^[63]

Growth



Juvenile *A. sp.* mount, Sam Noble
Oklahoma Museum of Natural
History

A 1999 microscopic study of *Apatosaurus* and *Brontosaurus* bones concluded the animals grew rapidly when young and reached near-adult sizes in about 10 years.^[67] In 2008, a study on the growth rates of sauropods was published by Thomas Lehman and Holly Woodward. They said that by using growth lines and length-to-mass ratios, *Apatosaurus* would have grown to 25 t (25 long tons; 28 short tons) in 15 years, with growth peaking at 5,000 kg (11,000 lb) in a single year. An alternative method, using limb length and body mass, found *Apatosaurus* grew 520 kg (1,150 lb) per year, and reached its full mass before it was about 70 years old.^[68] These estimates have been called unreliable because the calculation methods are not sound; old growth lines would have been obliterated by bone remodelling.^[69] One of the first identified growth factors of *Apatosaurus*

was the number of sacral vertebrae, which increased to five by the time of the creature's maturity. This was first noted in 1903 and again in 1936.^[5]

Long-bone histology enables researchers to estimate the age that a specific individual reached. A study by Eva Griebeler et al. (2013) examined long-bone histological data and concluded the *Apatosaurus* sp. SMA 0014 weighed 20,206 kg (22.3 short tons), reached sexual maturity at 21 years, and died aged 28. The same growth model indicated *Apatosaurus* sp. BYU 601–17328 weighed 18,178 kg (20.0 short tons), reached sexual maturity at 19 years, and died aged 31.^[69]

Juveniles

Compared with most sauropods, a relatively large amount of juvenile material is known from *Apatosaurus*. Multiple specimens in the OMNH are from juveniles of an undetermined species of *Apatosaurus*; this material includes partial shoulder and pelvic girdles, some vertebrae, and limb bones. OMNH juvenile material is from at least two different age groups and based on overlapping bones likely comes from more than three individuals. The specimens exhibit features that distinguish *Apatosaurus* from its relatives, and thus likely belong to the genus.^{[19][70]} Juvenile sauropods tend to have proportionally shorter necks and tails, and a more pronounced forelimb-hindlimb disparity than found in adult sauropods.^[71]

Tail

An article published in 1997 reported research of the mechanics of *Apatosaurus* tails by Nathan Myhrvold and paleontologist Philip J. Currie. Myhrvold carried out a computer simulation of the tail, which in diplodocids like *Apatosaurus* was a very long, tapering structure resembling a bullwhip. This computer modeling suggested diplodocids were capable of producing a whiplike cracking sound of over 200 decibels, comparable to the volume of a cannon being fired.^[72]

A pathology has been identified on the tail of *Apatosaurus*, caused by a growth defect. Two caudal vertebrae are seamlessly fused along the entire articulating surface of the bone, including the arches of the neural spines. This defect might have been caused by the lack or inhibition of the substance that forms intervertebral disks or joints.^[73] It has been proposed that the whips could have been used in combat and defense, but the tails of diplodocids were quite light and narrow compared to *Shunosaurus* and *mamenchisaurids*, and thus to injure another animal with the tail would severely injure the tail itself.^[72]

Paleoecology

The Morrison Formation is a sequence of shallow marine and alluvial sediments which, according to radiometric dating, dates from between 156.3 mya at its base,^[74] and 146.8 mya at the top,^[75] placing it in the late Oxfordian, Kimmeridgian, and early Tithonian stages of the Late Jurassic period. This formation is interpreted as originating in a locally semiarid environment with distinct wet and dry seasons. The Morrison Basin, where dinosaurs lived, stretched from New Mexico to Alberta and Saskatchewan; it was formed when the precursors to the Front Range of the Rocky Mountains started pushing up to the west. The deposits from their east-facing drainage basins were carried by streams and rivers and deposited in swampy lowlands, lakes, river channels, and floodplains.^[76] This formation is similar in age to the Lourinhã Formation in Portugal and the Tendaguru Formation in Tanzania.^[25]



Ischium of an *Apatosaurus* showing bite marks from a large theropod

Apatosaurus was the second most common sauropod in the Morrison Formation ecosystem, after *Camarasaurus*.^[45]

Apatosaurus may have been more solitary than other Morrison Formation dinosaurs.^[77] Fossils of the genus have only been found in the upper levels of the formation. Those of *Apatosaurus ajax* are known exclusively from the upper Brushy Basin Member, about 152–151 mya. *A. louisae* fossils are rare, known only from one site in the upper Brushy Basin Member; they date to the late Kimmeridgian stage, about 151 mya. Additional *Apatosaurus* remains are known from similarly aged or

slightly younger rocks, but they have not been identified as any particular species,^[78] and thus may instead belong to *Brontosaurus*.^[21]

The Morrison Formation records a time when the local environment was dominated by gigantic sauropod dinosaurs.^[45] Dinosaurs known from the Morrison Formation include the theropods *Allosaurus*, *Ceratosaurus*, *Ornitholestes*, *Saurophaganax*, and *Torvosaurus*; the sauropods *Brontosaurus*, *Brachiosaurus*, *Camarasaurus*, and *Diplodocus*; and the ornithischians *Camptosaurus*, *Dryosaurus*, and *Stegosaurus*.^[79] *Apatosaurus* is commonly found at the same sites as *Allosaurus*, *Camarasaurus*, *Diplodocus*, and *Stegosaurus*.^[77] *Allosaurus* accounted for 70–75% of theropod specimens and was at the top trophic level of the Morrison food web.^[80] Many of the dinosaurs of the Morrison Formation are of the same genera as those seen in Portuguese rocks of the Lourinhã Formation – mainly *Allosaurus*, *Ceratosaurus*, and *Torvosaurus* – or have a close counterpart – *Brachiosaurus* and *Lusotitan*, *Camptosaurus* and *Draconyx*, and *Apatosaurus* and *Dinheirosaurus*.^[25] Other vertebrates that are known to have shared this paleo-environment include ray-finned fishes, frogs, salamanders, turtles, sphenodonts, lizards, terrestrial and aquatic crocodylomorphans, and several species of pterosaur. Shells of bivalves and aquatic snails are also common. The flora of the period has been evidenced in fossils of green algae, fungi, mosses, horsetails, cycads, ginkgoes, and several families of conifers. Vegetation varied from river-lining forests of tree ferns with fern understory (gallery forests), to fern savannas with occasional trees such as the *Araucaria*-like conifer *Brachyphyllum*.^[81]



Saurophaganax and *A. ajax*, Sam Noble Oklahoma Museum of Natural History

References

1. Taylor, M.P. (2010). "Sauropod dinosaur research: a historical review." Pp. 361-386 in Moody, R.T.J.,

- Buffetaut, E., Naish, D. and Martill, D.E. (eds.), *Dinosaurs and Other Extinct Saurians: A Historical Perspective*. London: The Geological Society, Special Publication No. 34.
2. Berman, D.S. and McIntosh, J. S. (1978). "Skull and relationships of the Upper Jurassic sauropod *Apatosaurus* (Reptilia, Saurischia)." *Bulletin of the Carnegie Museum*, **8**: 1–35.
3. "Apatosaurus" (<https://www.merriam-webster.com/dictionary/Apatosaurus>). *Merriam-Webster Dictionary*.
4. "Apatosaurus" (<https://www.dictionary.com/browse/Apatosaurus>). *Dictionary.com Unabridged*. Random House.
5. Gilmore, C.W. (1936). "Osteology of *Apatosaurus*, with special references to specimens in the Carnegie Museum". *Memoirs of the Carnegie Museum*. **11** (4): 1–136. OCLC 16777126 (<https://www.worldcat.org/oclc/16777126>).
6. Seebacher, F. (2001). "A new method to calculate allometric length-mass relationships of dinosaurs" (http://dinoweb.ucoz.ru/_fr/4/A_new_method_to.pdf) (PDF). *Journal of Vertebrate Paleontology*. **21** (1): 51–52. CiteSeerX 10.1.1.462.255 (<https://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.462.255>). doi:10.1671/0272-4634(2001)021[0051:ANMTCA]2.0.CO;2 (<https://doi.org/10.1671%2F0272-4634%282001%29021%5B0051%3AANMTCA%5D2.0.CO%3B2>). ISSN 0272-4634 (<https://www.worldcat.org/issn/0272-4634>). JSTOR 4524171 (<https://www.jstor.org/stable/4524171>).
7. Mazzetta, G.V.; Christiansen, P.; Farina, R.A. (2004). "Giants and bizzarres: body size of some southern South American Cretaceous dinosaurs" (http://www.miketaylor.org.uk/tmp/papers/Mazzetta-et-al_04_SA-dino-body-size.pdf) (PDF). *Historical Biology*. **16** (2–4): 71–83. CiteSeerX 10.1.1.694.1650 (<https://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.694.1650>). doi:10.1080/08912960410001715132 (<https://doi.org/10.1080%2F08912960410001715132>). ISSN 1029-2381 (<https://www.worldcat.org/issn/1029-2381>).
8. Henderson, D.M. (2006). "Burly Gaits: Centers of mass, stability, and the trackways of sauropod dinosaurs". *Journal of Vertebrate Paleontology*. **26** (4): 907–921. doi:10.1671/0272-4634(2006)26[907:BGCOMS]2.0.CO;2 (<https://doi.org/10.1671%2F0272-4634%282006%2926%5B907%3ABGCOMS%5D2.0.CO%3B2>). JSTOR 4524642 (<https://www.jstor.org/stable/4524642>).
9. Bates, K.T.; Falkingham, P.L.; Macaulay, S.; Brassey, C.; Maidment, S.C.R. (2015). "Downsizing a giant: re-evaluating *Dreadnoughtus* body mass" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4528471>). *Biology Letters*. **11** (6): 20150215. doi:10.1098/rsbl.2015.0215 (<https://doi.org/10.1098%2Frsbl.2015.0215>). ISSN 1744-957X (<https://www.worldcat.org/issn/1744-957X>). PMC 4528471 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4528471>). PMID 26063751 (<https://pubmed.ncbi.nlm.nih.gov/26063751>).
10. Wedel, M. (2013). "A giant, skeletally immature individual of *Apatosaurus* from the Morrison Formation of Oklahoma" (<https://sauroposeidon.files.wordpress.com/2010/04/wedel-2013-svpca-giant-apatosaurus-from-oklahoma.pdf>) (PDF). *61st Symposium on Vertebrate Palaeontology and Comparative Anatomy - Programme and Abstracts*: 40–45.
11. Fastovsky, D.E.; Weishampel, D.B. (2009). *Dinosaurs: A Concise Natural History* (https://web.archive.org/web/20150924004505/http://www.evolbiol.ru/large_files/dinosaurs2009.pdf) (PDF). Cambridge University Press. pp. 165–200. ISBN 978-0-521-88996-4. Archived from the original (http://www.evolbiol.ru/large_files/dinosaurs2009.pdf) (PDF) on 24 September 2009.
12. Whitlock, J.A. (2011). "Inferences of Diplodocoid (Sauropoda: Dinosauria) Feeding Behavior from Snout Shape and Microwear Analyses" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3071828>). *PLOS ONE*. **6** (4): e18304. Bibcode:2011PLoSO...618304W (<https://ui.adsabs.harvard.edu/abs/2011PLoSO...618304W>). doi:10.1371/journal.pone.0018304 (<https://doi.org/10.1371%2Fjournal.pone.0018304>). PMC 3071828 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3071828>). PMID 21494685 (<https://pubmed.ncbi.nlm.nih.gov/21494685>).
13. Balanoff, A.M.; Bever, G.S.; Ikejiri, T. (2010). "The Braincase of *Apatosaurus* (Dinosauria: Sauropoda) Based on Computed Tomography of a New Specimen with Comments on Variation and Evolution in Sauropod Neuroanatomy" (<http://digitallibrary.amnh.org/bitstream/2246/6040/1/N3677.pdf>) (PDF). *American Museum Novitates*. **3677** (3677): 1–32. doi:10.1206/591.1 (<https://doi.org/10.1206%2F591.1>).
14. Taylor, M.P.; Wedel, M.J.; Naish, Darren; Engh, B. (2015). "Were the necks of *Apatosaurus* and *Brontosaurus* adapted for combat?" (<https://doi.org/10.7287/peerj.preprints.1347v1>). *PeerJ PrePrints*. **3**: e1663. doi:10.7287/peerj.preprints.1347v1 (<https://doi.org/10.7287%2Fpeerj.preprints.1347v1>).

15. Riggs, E.S. (1903). "Structure and Relationships of Opisthocoelian Dinosaurs. Part I, *Apatosaurus* Marsh" (http://www.miketaylor.org.uk/tmp/Riggs-1903_Structure%20and%20relationships%20of%20opisthocoelian%20dinosaurs.%20Part%20I.%20Apatosaurus%20Marsh.pdf) (PDF). *Publications of the Field Columbian Museum Geographical Series*. **2** (4): 165–196. OCLC 494478078 (<https://www.worldcat.org/oclc/494478078>).
16. Lovelace, D.M.; Hartman, S.A.; Wahl, W.R. (2007). "Morphology of a specimen of *Supersaurus* (Dinosauria, Sauropoda) from the Morrison Formation of Wyoming, and a re-evaluation of diplodocid phylogeny" (<https://www.academia.edu/539710>). *Arquivos do Museu Nacional*. **65** (4): 527–544. CiteSeerX 10.1.1.603.7472 (<https://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.603.7472>). ISSN 0365-4508 (<https://www.worldcat.org/issn/0365-4508>).
17. Upchurch, P. (1994). "Manus claw function in sauropod dinosaurs" (<http://www.arca.museum.ul.pt/ArcSite/obj/gaia/MNHNL-0000272-MG-DOC-web.PDF>) (PDF). *Gaia*. **10**: 161–171. ISSN 0871-5424 (<https://www.worldcat.org/issn/0871-5424>).
18. Martin, A.J. (2006). *Introduction to the Study of Dinosaurs (Second ed.)* (<https://archive.org/details/introductiontost00mart>). Blackwell Publishing. p. 560 (<https://archive.org/details/introductiontost00mart/page/n576>). ISBN 978-1-4051-3413-2.
19. Upchurch, P.; Tomida, Y.; Barrett, P.M. (2005). "A new specimen of *Apatosaurus ajax* (Sauropoda: Diplodocidae) from the Morrison Formation (Upper Jurassic) of Wyoming, USA" (<http://ci.nii.ac.jp/naid/110004665753/>). *National Science Museum Monographs*. **26** (118): 1–156. ISSN 1342-9574 (<http://www.worldcat.org/issn/1342-9574>).
20. Marsh, O.C. (1877). "Notice of New Dinosaurian Reptiles from the Jurassic formation" (<http://marsh.dinodb.com/marsh/Marsh%201877%20-%20Notice%20of%20new%20dinosaurian%20reptiles%20from%20the%20Jurassic%20formation.pdf>) (PDF). *American Journal of Science*. **14** (84): 514–516. Bibcode:1877AmJS...14..514M (<https://ui.adsabs.harvard.edu/abs/1877AmJS...14..514M>). doi:10.2475/ajs.s3-14.84.514 (<https://doi.org/10.2475%2Fajs.s3-14.84.514>).
21. Tschopp, E.; Mateus, O. V.; Benson, R. B. J. (2015). "A specimen-level phylogenetic analysis and taxonomic revision of Diplodocidae (Dinosauria, Sauropoda)" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4393826>). *PeerJ*. **3**: e857. doi:10.7717/peerj.857 (<https://doi.org/10.7717%2Fpeerj.857>). PMC 4393826 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4393826>). PMID 25870766 (<https://pubmed.ncbi.nlm.nih.gov/25870766>).
22. Liddell, G.H.; Scott, R. (1882). *A Greek-English Lexicon* (<https://archive.org/stream/greekenglishlex00lidduoft#page/iv/mode/2up>). Harper & Brothers. pp. 1–1774.
23. Holtz, T.R. Jr. (2008). *Dinosaurs: The Most Complete, Up-to-Date Encyclopedia for Dinosaur Lovers of All Ages* (<https://archive.org/details/dinosaursmostcom00holt>). Random House. pp. 1 (<https://archive.org/details/dinosaursmostcom00holt/page/n8>)–432. ISBN 978-0-375-82419-7.
24. Marsh, O.C. (1879). "Notice of new Jurassic dinosaurs" (<http://marsh.dinodb.com/marsh/Marsh%201879%20-%20Notice%20of%20new%20Jurassic%20reptiles.pdf>) (PDF). *American Journal of Science*. **18** (108): 501–505. Bibcode:1879AmJS...18..501M (<https://ui.adsabs.harvard.edu/abs/1879AmJS...18..501M>). doi:10.2475/ajs.s3-18.108.501 (<https://doi.org/10.2475%2Fajs.s3-18.108.501>).
25. Mateus, O. (2006). "Jurassic dinosaurs from the Morrison Formation (USA), the Lourinhã and Alcobaça Formations (Portugal), and the Tendaguru Beds (Tanzania): A comparison". In Foster, John R.; Lucas, Spencer G. (eds.). *Paleontology and Geology of the Upper Jurassic Morrison Formation*. **36**. New Mexico Museum of Natural History and Science Bulletin. pp. 223–231.
26. Bakker, R.T. (1994). "The Bite of the Bronto" (<http://connection.ebscohost.com/c/articles/9409020826/bite-bronto>). *Earth*. **3** (6): 26–33.
27. Matthew, W.D. (1905). "The mounted skeleton of *Brontosaurus*" (<https://archive.org/stream/p2naturalhistory05ameruoft>). *The American Museum Journal*. **5** (2): 63–70.
28. McIntosh, J.S.; Berman, D.S. (1975). "Description of the Palate and Lower Jaw of the Sauropod Dinosaur *Diplodocus* (Reptilia: Saurischia) with Remarks on the Nature of the Skull of *Apatosaurus*". *Journal of Paleontology*. **49** (1): 187–199. JSTOR 1303324 (<https://www.jstor.org/stable/1303324>).
29. Miller, B. (2014-10-30). "Bully for *Camarasaurus*" (<https://dinosaurs.wordpress.com/2014/10/30/bully-for-camarasaurus/>). Dinosaurs.

30. Parsons, K.M. (1997). "The Wrongheaded Dinosaur" (https://web.archive.org/web/20100414165426/http://www.carnegiemuseums.org/cmaggbk_issue/1997/novdec/feat5.htm). Carnegie Magazine. Archived from the original (http://www.carnegiemuseums.org/cmaggbk_issue/1997/novdec/feat5.htm) on 14 April 2010.
31. Crafton, D.C. (1982). *Before Mickey: The Animated Film 1898–1928* (<http://www.micheleleighb.net/wp-content/uploads/2014/01/Crafton.pdf>) (PDF). MIT Press. pp. 1–57. ISBN 978-0-262-03083-0.
32. Glut, D.F. (1997). *Dinosaurs: The Encyclopedia* (https://archive.org/details/dinosaursencyclo04dfgl_143). McFarland. pp. 150 (https://archive.org/details/dinosaursencyclo04dfgl_143/page/n155)–163. ISBN 978-0-7864-7222-2.
33. Carpenter, Kenneth; Tidwell, Virginia (1998). "Preliminary Description of a Brachiosaurus Skull from Felch Quarry 1, Garden Park, Colorado" (https://books.google.com/books?id=CLEPeg_SjTcC&pg=PA69). In Carpenter, Kenneth; Chure, Dan; Kirkland, James Ian (eds.). *The Upper Jurassic Morrison Formation: an interdisciplinary study*. ISBN 978-90-5699-183-8.
34. Barrett, P.M.; Storrs, G.W.; Young, M.T.; Witmer, L.M. (2011). "A new skull of *Apatosaurus* and its taxonomic and palaeobiological implications" (<http://www.miketaylor.org.uk/dino/pubs/svpca2011/SVPCA2011-abstracts.pdf>) (PDF). *Symposium of Vertebrate Palaeontology & Comparative Anatomy Abstracts of Presentations*: 5.
35. Taylor, M.P. (2010). "Sauropod dinosaur research: a historical review" (<http://www.miketaylor.org.uk/dino/pubs/taylor2010/Taylor2010-sauropod-history.pdf>) (PDF). *Geological Society, London, Special Publications*. **343** (1): 361–386. Bibcode:2010GSLSP.343..361T (<https://ui.adsabs.harvard.edu/abs/2010GSLSP.343..361T>). doi:10.1144/SP343.22 (<https://doi.org/10.1144/2FSP343.22>).
36. Brinkman, P. (2006). "Bully for *Apatosaurus*". *Endeavour*. **30** (4): 126–130. doi:10.1016/j.endeavour.2006.10.004 (<https://doi.org/10.1016%2Fj.endeavour.2006.10.004>). PMID 17097734 (<https://pubmed.ncbi.nlm.nih.gov/17097734/>).
37. Upchurch, P.; Barrett, P.M.; Dodson, P. (2004). "Sauropoda". In Weishampel, David B.; Osmólska, Peter; Dodson, P. (eds.). *The Dinosauria* (<https://archive.org/details/dinosauriandedit00weis>) (2 ed.). University of California Press. pp. 259 (<https://archive.org/details/dinosauriandedit00weis/page/n277>)–322. ISBN 978-0-520-25408-4.
38. McIntosh, J.S. (1995). Sun, A.; Wang, Y. (eds.). "Remarks on the North American sauropod *Apatosaurus* Marsh". *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota Short Papers*: 119–123.
39. Bakker, R.T. (1998). "Dinosaur mid-life crisis: the Jurassic-Cretaceous transition in Wyoming and Colorado" (<http://econtent.unm.edu/cdm/ref/collection/bulletins/id/928>). In Lucas, Spencer G.; Kirkland, James I.; Estep, J.W. (eds.). *Lower and Middle Cretaceous Terrestrial Ecosystems*. **14**. New Mexico Museum of Natural History and Science Bulletin. pp. 67–77.
40. D'Emic, M. 2015. "Not so fast, Brontosaurus" (<http://time.com/3810104/not-so-fast-brontosaurus/>). Time.com
41. Prothero, D. 2015. "Is "Brontosaurus" Back? Not So Fast!" (<http://www.skeptic.com/insight/is-brontosaurus-back-not-so-fast/>). Skeptic.com.
42. Carpenter, Kenneth; Currie, P.J., eds. (1992). *Dinosaur Systematics, Approaches and Perspectives* (<https://archive.org/details/dinosaursystemat00carp>). Cambridge University Press. pp. 1 (<https://archive.org/details/dinosaursystemat00carp/page/n19>)–318. ISBN 978-0-521-36672-4.
43. Carpenter, K.; McIntosh, J. (1994). "Upper Jurassic sauropod babies from the Morrison Formation". In Carpenter, Kenneth; Hirsch, Karl F.; Horner, John R. (eds.). *Dinosaur Eggs and Babies*. Cambridge University Press. pp. 265–278. ISBN 978-0-521-56723-7.
44. Marsh, O.C. (1878). "Principal Characters of American Jurassic Dinosaurs" (<http://marsh.dinodb.com/marsh/Marsh%201878%20-%20Principle%20characters%20of%20American%20Jurassic%20dinosaurs,%20Part%20I.pdf>) (PDF). *American Journal of Science*. **16** (95): 412–414.
45. Foster, J. (2007). *Jurassic West: The Dinosaurs of the Morrison Formation and Their World*. Indiana University Press. pp. 273–329. ISBN 978-0-253-34870-8.
46. Taylor, M.P. (2012-07-27). "'*Apatosaurus* *minimus* sacrum/ilia, right lateral view" (<http://svpow.com/2012/06/27/apatosaurus-minimus-sacrumilia-right-lateral-view/>). Sauropod Vertebrae Picture of the Week.

47. Taylor, M.P.; Wedel, M.J. (2012). "Re-evaluating "Apatosaurus" *minimus*, a bizarre Morrison Formation sauropod with diplodocoid and macronarian features" (<http://www.miketaylor.org.uk/dino/pubs/svpca2012/abstract.html#gsc.tab=0>). *SVPCA 2012 Programme and Abstracts*: 23.
48. Taylor, M.P.; Naish, D. (2005). "The phylogenetic taxonomy of Diplodocoidea (Dinosauria: Sauropoda)" (<http://www.miketaylor.org.uk/dino/pubs/taylor-and-naish2005/TaylorNaish2005-diplodocoid-taxonomy.pdf>) (PDF). *PaleoBios*. **25** (2): 1–7.
49. Harris, J.D. (2006). "The significance of *Suuwassea emiliae* (Dinosauria: Sauropoda) for flagellicaudatan intrarelationships and evolution" (http://cactus.dixie.edu/jharris/Flagellicaudatan_Phylogeny.pdf) (PDF). *Journal of Systematic Palaeontology*. **4** (2): 185–198. doi:10.1017/S1477201906001805 (<https://doi.org/10.1017%2FS1477201906001805>).
50. Whitlock, J.A. (2011). "A phylogenetic analysis of Diplodocoidea (Saurischia: Sauropoda)" (<https://doi.org/10.1111/j.1096-3642.2010.00665.x>). *Zoological Journal of the Linnean Society*. **161** (4): 872–915. doi:10.1111/j.1096-3642.2010.00665.x (<https://doi.org/10.1111%2Fj.1096-3642.2010.00665.x>).
51. Gallina, P.A.; Apesteguía, S.; Haluza, A.; Canale, J.A. (2014). Farke, Andrew A. (ed.). "A Diplodocid Sauropod Survivor from the Early Cretaceous of South America" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4020797>). *PLOS ONE*. **9** (5): e97128. Bibcode:2014PLoSO...997128G (<https://ui.adsabs.harvard.edu/abs/2014PLoSO...997128G>). doi:10.1371/journal.pone.0097128 (<https://doi.org/10.1371%2Fjournal.pone.0097128>). PMC 4020797 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4020797>). PMID 24828328 (<https://pubmed.ncbi.nlm.nih.gov/24828328>).
52. Pierson, D.J. (2009). "The Physiology of Dinosaurs: Circulatory and Respiratory Function in the Largest Animals Ever to Walk the Earth". *Respiratory Care*. **54** (7): 887–911. doi:10.4187/002013209793800286 (<https://doi.org/10.4187%2F002013209793800286>). PMID 19558740 (<https://pubmed.ncbi.nlm.nih.gov/19558740>).
53. Stevens, K.A.; Parrish, J.M. (1999). "Neck Posture and Feeding Habits of Two Jurassic Sauropod Dinosaurs". *Science*. **284** (5415): 798–800. Bibcode:1999Sci...284..798S (<https://ui.adsabs.harvard.edu/abs/1999Sci...284..798S>). doi:10.1126/science.284.5415.798 (<https://doi.org/10.1126%2Fscience.284.5415.798>). PMID 10221910 (<https://pubmed.ncbi.nlm.nih.gov/10221910>).
54. Stevens, K.A.; Parrish, J.M. (2005). "Neck Posture, Dentition and Feeding Strategies in Jurassic Sauropod Dinosaurs". In Carpenter, Kenneth; Tidswell, Virginia (eds.). *Thunder Lizards: The Sauropodomorph Dinosaurs* (<https://archive.org/details/thunderlizardssa00tidw>). Indiana University Press. pp. 212 (<https://archive.org/details/thunderlizardssa00tidw/page/n224>)–232. ISBN 978-0-253-34542-4. OCLC 218768170 (<https://www.worldcat.org/oclc/218768170>).
55. Sellers, W.I.; Margetts, L.; Coria, R.A.; Manning, P.L. (2012). "March of the Titans: The Locomotor Capabilities of Sauropod Dinosaurs" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3864407>). *PLOS ONE*. **8** (10): e78733. Bibcode:2013PLoSO...878733S (<https://ui.adsabs.harvard.edu/abs/2013PLoSO...878733S>). doi:10.1371/journal.pone.0078733 (<https://doi.org/10.1371%2Fjournal.pone.0078733>). PMC 3864407 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3864407>). PMID 24348896 (<https://pubmed.ncbi.nlm.nih.gov/24348896>).
56. Switek, B. (November 2, 2010). "Did Wee Little Sauropods Stand Up to Run?" (<http://www.smithsonianmag.com/science-nature/did-wee-little-sauropods-stand-up-to-run-85531831/?no-ist>). Smithsonian.com. Retrieved September 20, 2015.
57. "Tracks of a running bipedal baby brontosaurus? Baby sauropod footprints discovered in Colorado" (<https://www.sciencedaily.com/releases/2010/11/101101083150.htm>). Science Daily (The Geological Society of America). November 1, 2010. Retrieved September 20, 2015.
58. Upchurch, P.; et al. (2000). "Neck Posture of Sauropod Dinosaurs" (<http://www.sciencemag.org/cgi/reprint/287/5453/547b.pdf>) (PDF). *Science*. **287** (5453): 547b. doi:10.1126/science.287.5453.547b (<https://doi.org/10.1126%2Fscience.287.5453.547b>). Retrieved 2008-08-05.
59. Taylor, M.P. (2014). "Quantifying the effect of intervertebral cartilage on neutral posture in the necks of sauropod dinosaurs" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4277489>). *PeerJ*. **2**: e712. doi:10.7717/peerj.712 (<https://doi.org/10.7717%2Fpeerj.712>). PMC 4277489 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4277489>). PMID 25551027 (<https://pubmed.ncbi.nlm.nih.gov/25551027>).
60. Taylor, M.P.; Wedel, M.J.; Naish, D. (2009). "Head and neck posture in sauropod dinosaurs inferred from extant animals" (<http://www.app.pan.pl/archive/published/app54/app54-213.pdf>) (PDF). *Acta Palaeontologica Polonica*. **54** (2): 213–220. doi:10.4202/app.2009.0007 (<https://doi.org/10.4202%2Fapp.2009.0007>).

61. Cobley, M.J.; Rayfield, E.J.; Barrett, P.M. (2013). "Inter-Vertebral Flexibility of the Ostrich Neck: Implications for Estimating Sauropod Neck Flexibility" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3743800>). *PLOS ONE*. **8** (8): e72187. Bibcode:2013PLoSO...872187C (<https://ui.adsabs.harvard.edu/abs/2013PLoSO...872187C>). doi:10.1371/journal.pone.0072187 (<https://doi.org/10.1371%2Fjournal.pone.0072187>). PMC 3743800 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3743800>). PMID 23967284 (<https://pubmed.ncbi.nlm.nih.gov/23967284>).
62. Ghose, T. (August 15, 2013). "Ouch! Long-Necked Dinosaurs Had Stiff Necks" (<http://www.livescience.com/38895-sauropods-had-stiff-necks.html>). livescience.com. Retrieved January 31, 2015.
63. Paladino, F.V.; Spotila, J.R.; Dodson, P. (1997). "A Blueprint for Giants: Modeling the Physiology of Large Dinosaurs". In Farlow, J.O.; Brett-Surman, M.K. (eds.). *The Complete Dinosaur* (https://archive.org/details/isbn_9780253333490/page/491). Indiana University Press. pp. 491–504 (https://archive.org/details/isbn_9780253333490/page/491). ISBN 978-0-253-33349-0.
64. Wedel, M.J. (2003). "Vertebral Pneumaticity, Air Sacs, and the Physiology of Sauropod Dinosaurs". *Paleobiology*. **29** (2): 243–255. doi:10.1666/0094-8373(2003)029<0243:vpasat>2.0.co;2 (<https://doi.org/10.1666%2F0094-8373%282003%29029%3C0243%3Avpasat%3E2.0.co%3B2>). JSTOR 4096832 (<https://www.jstor.org/stable/4096832>).
65. Spotila, J.R.; O'Connor, M.P.; Dodson, P.R.; Paladino, F.V. (1991). "Hot and cold running dinosaurs. Metabolism, body temperature, and migration". *Modern Geology*. **16**: 203–227.
66. Farlow, J.A. (1987). "Speculations About the Diet and Physiology of Herbivorous Dinosaurs". *Paleobiology*. **13** (1): 60–72. doi:10.1017/S0094837300008587 (<https://doi.org/10.1017%2FS0094837300008587>). JSTOR 2400838 (<https://www.jstor.org/stable/2400838>).
67. Curry, K.A. (1999). "Ontogenetic histology of *Apatosaurus* (Dinosauria: Sauropoda): new insights on growth rates and longevity". *Journal of Vertebrate Paleontology*. **19** (4): 654–665. doi:10.1080/02724634.1999.10011179 (<https://doi.org/10.1080%2F02724634.1999.10011179>). JSTOR 4524036 (<https://www.jstor.org/stable/4524036>).
68. Lehman, T.M.; Woodward, H.N. (2008). "Modelling growth rates for sauropod dinosaurs". *Paleobiology*. **34** (2): 264–281. doi:10.1666/0094-8373(2008)034[0264:MGRFSD]2.0.CO;2 (<https://doi.org/10.1666%2F0094-8373%282008%29034%5B0264%3AMGRFSD%5D2.0.CO%3B2>).
69. Griebeler, E.M.; Klein, N.; Sander, P.M. (2013). "Aging, Maturation and Growth of Sauropodomorph Dinosaurs as Deduced from Growth Curves Using Long Bone Histological Data: An Assessment of Methodological Constraints and Solutions" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3686781>). *PLOS ONE*. **8** (6): e67012. Bibcode:2013PLoSO...867012G (<https://ui.adsabs.harvard.edu/abs/2013PLoSO...867012G>). doi:10.1371/journal.pone.0067012 (<https://doi.org/10.1371%2Fjournal.pone.0067012>). PMC 3686781 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3686781>). PMID 23840575 (<https://pubmed.ncbi.nlm.nih.gov/23840575>).
70. Carpenter, K.; McIntosh, J.S. (1994). Carpenter, Kenneth; Hirsch, Karl. F.; Horner, John R. (eds.). *Dinosaur Eggs and Babies*. Cambridge University Press. pp. 265–274. ISBN 978-0-521-44342-5.
71. Wedel, M. (2013). "Get down, get fuzzy, speculative juvenile *Apatosaurus*!" (<http://svpow.com/2013/02/27/get-down-get-fuzzy-speculative-juvenile-apatosaurus/>). SVPOW.
72. Myhrvold, N.P.; Currie, P.J. (1997). "Supersonic sauropods? Tail dynamics in the diplodocids". *Paleobiology*. **23** (4): 393–409. doi:10.1017/S0094837300019801 (<https://doi.org/10.1017%2FS0094837300019801>). JSTOR 2401127 (<https://www.jstor.org/stable/2401127>).
73. Lovelace, D.M. (2014). "Developmental Failure of Segmentation in a Caudal Vertebra of *Apatosaurus* (Sauropoda)". *The Anatomical Record*. **297** (7): 1262–1269. doi:10.1002/ar.22887 (<https://doi.org/10.1002%2Far.22887>). PMID 24532488 (<https://pubmed.ncbi.nlm.nih.gov/24532488>).
74. Trujillo, K.C.; Chamberlain, K.R.; Strickland, A. (2006). "Oxfordian U/Pb ages from SHRIMP analysis for the Upper Jurassic Morrison Formation of southeastern Wyoming with implications for biostratigraphic correlations". *Geological Society of America Abstracts with Programs*. **38** (6): 7.
75. Bilbey, S.A. (1998). "Cleveland-Lloyd Dinosaur Quarry - age, stratigraphy and depositional environments". In Carpenter, K.; Chure, D.; Kirkland, J.I. (eds.). *The Morrison Formation: An Interdisciplinary Study*. Modern Geology **22**. Taylor and Francis Group. pp. 87–120. ISSN 0026-7775 (<https://www.worldcat.org/issn/0026-7775>).
76. Russell, D.A. (1989). *An Odyssey in Time: Dinosaurs of North America*. Minocqua, Wisconsin: NorthWord Press. pp. 64–70. ISBN 978-1-55971-038-1.

77. Dodson, P.; Behrensmeyer, A.K.; Bakker, R.T.; McIntosh, J.S. (1980). "Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation". *Paleobiology*. **6** (2): 208–232. doi:10.1017/S0094837300025768 (<https://doi.org/10.1017%2FS0094837300025768>).
78. Turner, C.E.; Peterson, F. (1999). "Biostratigraphy of dinosaurs in the Upper Jurassic Morrison Formation of the Western Interior, U.S.A.". In Gillette, D.D. (ed.). *Vertebrate Paleontology in Utah*. Utah Geological Survey Miscellaneous Publication. pp. 77–114.
79. Chure, D.J.; Litwin, R.; Hasiotis, S.T.; Evanoff, E.; Carpenter, K. (2006). "The fauna and flora of the Morrison Formation: 2006". In Foster, John R.; Lucas, Spencer G. (eds.). *Paleontology and Geology of the Upper Jurassic Morrison Formation*. **36**. New Mexico Museum of Natural History and Science Bulletin. pp. 233–248.
80. Foster, J.R. (2003). *Paleoecological Analysis of the Vertebrate Fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain Region, U.S.A.* **23**. New Mexico Museum of Natural History and Science Bulletin. p. 29.
81. **Carpenter, K.** (2006). "Biggest of the big: a critical re-evaluation of the mega-sauropod *Amphicoelias fragillimus*". In Foster, John R.; Lucas, Spencer G. (eds.). *Paleontology and Geology of the Upper Jurassic Morrison Formation*. **36**. New Mexico Museum of Natural History and Science Bulletin. pp. 131–138.

External links

- Hartman, S. (2013). "Sauropods and kin" (<http://skeletaldrawing.com/sauropods-and-kin/>). Scott Hartman's Skeletal Drawings.
 - Batuman, Elif. Brontosaurus Rising (<http://www.newyorker.com/tech/elements/apatosaurus-brontosaurus-rising>) (April 2015), *The New Yorker*
 - Krystek, Lee. "Whatever Happened to the Brontosaurus?" (<http://www.unmuseum.org/dinobront.htm>) UnMuseum (Museum of Unnatural Mystery), 2002.
 - Taylor, Mike. "Why is 'Brontosaurus' now called *Apatosaurus*?" (<http://www.miketaylor.org.uk/dino/faq/s-class/bronto/>) MikeTaylor.org.uk, June 28, 2004.
-

Retrieved from "<https://en.wikipedia.org/w/index.php?title=Apatosaurus&oldid=967160087>"

This page was last edited on 11 July 2020, at 14:05 (UTC).

Text is available under the [Creative Commons Attribution-ShareAlike License](#); additional terms may apply. By using this site, you agree to the [Terms of Use](#) and [Privacy Policy](#). Wikipedia® is a registered trademark of the [Wikimedia Foundation, Inc.](#), a non-profit organization.